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STAHLECKERIA LENZII, A GIANT TRIASSIC BRAZILIAN DICYNODONT

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No. 4.—*Stahleckeria lenzii, a giant Triassic Brazilian Dicynodont*

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The Harvard collection of Triassic reptiles from southern Brazil contrasts strongly with that of von Huene (1935) in the nature of the contained dicynodont material. His finds from Chiniqua included only a small amount of dicynodont remains of which the greater part belonged to the giant form *Stahleckeria potens.* Our materials from a similar faunal horizon at Candelaria include a great variety of complete and partial skeletons of more modest size. Of remains of large animals, we have but a partial skeleton, which is described below. While comparable with *S. potens* in size and certain general characteristics, our specimen, as will be seen, differs in a number of features suggesting that it is specifically if not generically distinct, and it is therefore described below as *Stahleckeria lenzii,* sp. nov. The specimen (M. C. Z. no. 1688) comes from the Municipio de Candelaria, State of Rio Grande do Sul, Brazil, and from an Upper Triassic formation.

SKULL

Of the skull, the portion preserved (Figs. 1–4) is essentially the right posterior quadrant, relatively little crushed and for the most part well preserved and showing good surface detail in many areas. Anteriorly the zygomatic arch is broken off across the squamosal-jugal suture. Medially the anterior termination is roughly through the pituitary region; dorsally however, the broken surface slants backward so that the "sagittal crest" is incomplete. Medially the portion preserved extends well beyond the mid-line for much of the height of the braincase. In occipital view may be seen the occipital plate, well preserved on the right side and complete except for a small portion of the supraoccipital. Presumably the normal elements—basi-, ex- and supraoccipitals and opisthotic—are present, but sutures are not discernible. The plate is relatively much narrower than that of *S. potens* figured by von Huene. The foramen magnum as preserved is quite narrow, but this is probably due to transverse compression. Below this opening is the condyle, gently convex, with a notochordal depression, subcircular in outline but with dorso-lateral expansions in the presumed exoccipital areas. The dorsal portions of the exoccipitals are poorly preserved. The vagus foramen is present, continued latero-ventrally by a well marked groove, but data on the hypoglossal is lacking. Just anterior to the condyle are the heavy and pronounced ventral tubera, characteristic of dicynodonts, which descend to surround the median and posterior borders of the fenestra ovalis. Certainly these processes are formed in great measure by the basioccipital; von Huene indicates a suture which suggests that they are entirely formed by that element.

The paroccipital process, presumably formed on its posterior aspect by the opisthotic is short but very broad distally and much thickened ventrally. The ventral portion of the distal end abuts against a broad medially directed flange of the squamosal. The ventro-lateral corner of the process approaches the quadrate closely just above the inner portion of the articular surface of that bone and at the same point is close to the distal end of the stapes. The thinner upper portion of the paroccipital process is applied to the posterior surface of the squamosal. At the upper end of the paroccipital process there is a small notch in the lateral border of the occipital plate which forms the medial margin of the posterior opening of the posttemporal fenestra. This opening lies at the bottom of a deep triangular pocket. The outer margin of this pocket is formed by a vertical flange on the squamosal, the upper wall by a strong ridge on the conjoined supraoccipital and squamosal, while the paroccipital forms the more gently sloping medial boundary.

Von Huene's figure indicates a somewhat different build of the paroccipital region in *S. potens* (See our Fig. 6). The thicker portion of the distal end shows in our specimen an incipient subdivision into two portions. In von Huene's figured specimen there appears to be a sharp subdivision of these two areas, with the upper subdivision flaring widely backward at its distal end. The thin upper portion appears not to extend so far laterally below the posttemporal fenestra in his figured specimen as in ours.

The supraoccipital extends far dorsally and laterally as a relatively thin sheet of bone which gains contact at its outer margins with the adjacent dermal elements. The more lateral portion is ensheathed by the squamosal, which covers the posterior (as well as the anterior) surface of the bone, a feature not shown in von Huene's illustrated specimen. A pronounced ridge runs from the exoccipital region outward and upward above the posttemporal fenestra; this ridge is continued outward by the ensheathing portion of the squamosal. Dorsally the supraoccipital is in contact with the interparietal. The dorsal margin is imperfect and details are uncertain, although presumably of normal dicynodont type.

An anterior view of the temporal region (Fig. 1) shows the considerable extent to which the lateral portion of the occipital and otic regions are overlapped anteriorly by the squamosal. Above the posttemporal fenestra the squamosal appears to be closely attached to the braincase, although an irregular sutural line marks the most antero-

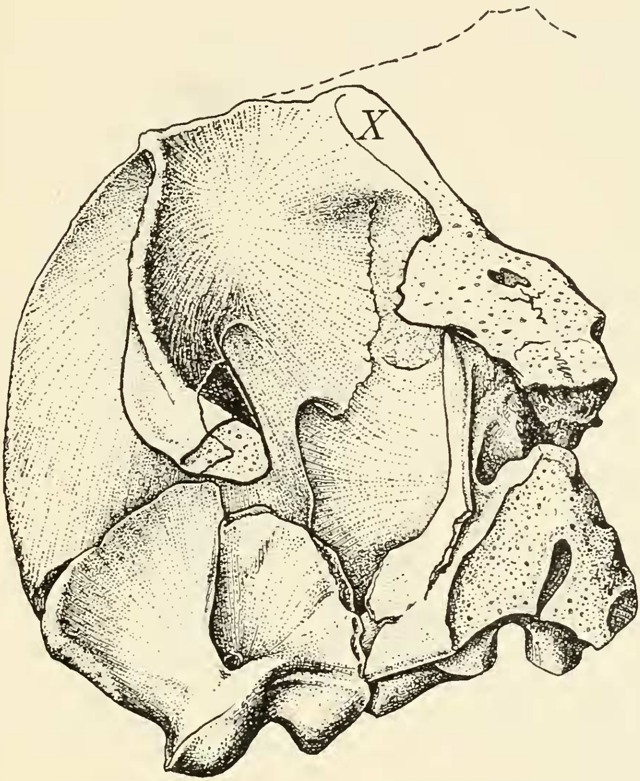

Fig. 1. *Stahleckeria lenzii*, anterior view of right temporal region. x 1/4.

medial extension of that bone. The squamosal curves away from the surface of the braincase for a short distance to form the lateral wall of the anterior opening of the posttemporal fenestra. Below the fenestra the squamosal extends downward to sheath completely the anterior face of the distal end of the paroccipital process. The connection here, however, was obviously less firm, and the paroccipital appears to have had some slight amount of "play" on the squamosal.

As regards the composition of the lateral or anterior aspect of the otic region, it seems reasonable to assume that the lower and middle portions are formed, in normal fashion, by the proötic. On this aspect, rather far ventrally (and concealed in the figures by the lower end of the epipterygoid) is a foramen, presumably for the facial nerve, leading into a backwardly directed groove. Up to a point well above the supratemporal the region is well ossified, the surface a smooth perichondral layer. Above this point, in an area bounded posteriorly by the squamosal and dorsally by the parietal, the braincase wall is filled out by a loose spongy ossification, obviously laid down in cartilage. This area is an open one in primitive synapsids; here, as in other progressive therapsids, there has occurred a new growth of otic cartilage, followed by a feeble ossification. Whether this ossification proceeds from the proötic center or that of the supraoccipital cannot be determined here. In this feebly ossified area there is some indication of a foramen, presumably venous, near the ventro-lateral corner and continuous with a broad groove on the proötic leading downward and outward toward the posttemporal fenestra. Anteriorly there is some indication of an anterior termination of this feeble ossification in the region of the presumed incisure for the trigeminal nerve, medial to the ascending ramus of the epipterygoid.

Our interpretation of this lateral aspect of the otic region differs in a few regards from that of von Huene for *S. potens* (his Fig. 4). He indicates a definite suture between pro- and opisthotic which we have failed to find, and includes the problematical spongy region seen in our skull in the opisthotic area. On the ventral surface of the braincase the basioccipital continues forward in a deep groove between the tubera for the fenestrae ovales to a distinct suture with an element which appears to be dermal in nature and interpretable as the parasphenoid.

The fenestra ovalis is, as typically in the group, at the end of a prominent ventrally directed bony funnel, and opens almost directly downward. The fenestra, as preserved, is oval in shape, with the long axis antero-posterior. As noted above, the medial and posterior margins are formed by a very thick wall of bone of crescentic outline, formed in part, if not entirely, by the basioccipital. The lateral margin is formed by a much thinner ventral extension from the otic region, but whether opisthotic or proötic cannot be said. The anterior surface of the otic region slopes smoothly down and back toward this rim, but in addition there is a short diagonal ridge connecting the rim with the ventral edge of the base of the paroccipital process. The anterior margins of the fenestrae are closed by the parasphenoid which forms "tubera basisphenoidales" closely comparable with those of more primitive

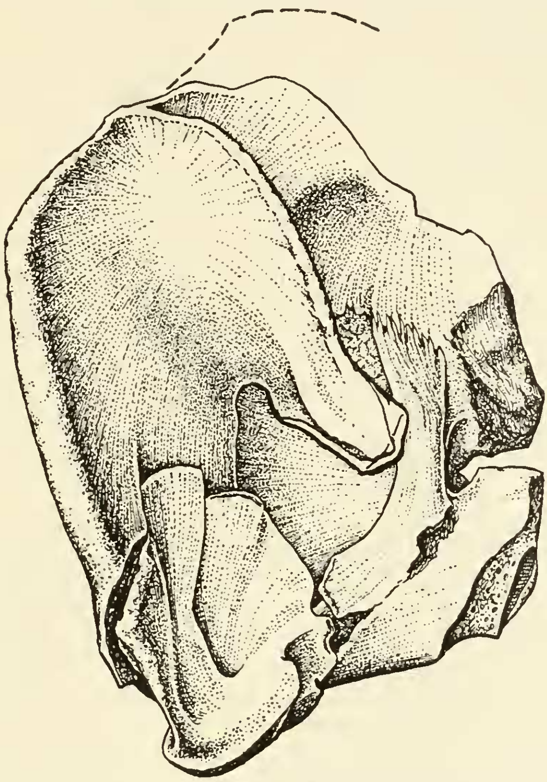

Fig. 2. As Figure 1, lateral view, x 1/4.

reptiles. The exposed (posterior) portion of the parasphenoid is triangular in outline ventrally, with a broad posterior base including the tubera and the intervening valley, and a convergence anteriorly to a point where the bone disappears between the pterygoids.

The preserved portion of the braincase terminates anteriorly at an irregular fracture through the general level of the pituitary. Little can be definitely determined concerning the structure here. An unossified incisure obviously indicates the position of the sella turcica. Ventral to this the basisphenoid presumably is included centrally in a mass of bone of which the pterygoids contribute the lateral portions. Dorsal to the incisure is a thick mass of spongy bone which probably includes a posterior extension of the "ethmoid" although presumably for the most part composed of descending processes of the parietals.

Since our skull is incomplete dorsally in the mid-line, the parietal region cannot be fully described. The contours in the otic region suggest strongly that there was a relatively narrow "sagittal crest" between the temporal fossae rather than the relatively broad parietal region seen in *S. potens*.

The broad mass of bone lying above the epipterygoid region appears to pertain, in great measure at least, to the parietals. It is perforated by the "shaft" descending from the pineal opening and there is evidence of a median suture. The bone is, however, quite spongy in texture, suggesting that the parietal has not simply sent down a dermal flange but has invaded the more dorsal portion of the chondrocranium. Curving around the anterior side of the pineal "shaft" is a more or less distinct crescentic area of bone which may possibly represent a deep portion of a preparietal. The most anterior part of this same mass of bone is more difficult of interpretation. It consists of paired areas of spongy bone which most probably represent posterior lateral extensions from the "ethmoid".

The ventral boundary of the parietal can be traced for some distance along the upper margin of the lateral surface of the braincase. This boundary extends from a contact with the upper end of the epipterygoid backward and upward around the poorly ossified area of the otic region discussed earlier. The exact extent of the postero-lateral development of the parietal along the "occipital crest" is somewhat uncertain. On the anterior surface of this region the parietal tapers out to a point above an antero-medial projection of the squamosal and below a mass of bone of uncertain nature, discussed below. The posterior face of this postero-lateral extension of the parietal is applied closely to the anterior surface of the supraoccipital.

Due to lack of preservation along the mid-line dorsally, only the lateral termination of the interparietal is preserved. This is a thin sheet of bone overlapping the most medial and dorsal corner of the squamosal and in contact below with the supraoccipital. The contours of this region suggest that the interparietal took part in the formation of a median crest, as is the case in many other dicynodonts. Von

Huene, however, figures the interparietal in *S. potens* as occupying a markedly depressed median area, above a depressed and grooved central portion of the supraoccipital. This depression is, however, highly comparable to that which in other forms in our collections receives the interparietal, an element which tends to be fairly readily separable from the occipital plate. It is perhaps possible that von Huene's figured specimen has lost the interparietal, and that the outlines given by him for this bone are in reality the impressions of its margins left upon the underlying elements.

A tabular is frequently recorded in dicynodonts and von Huene has indicated one in *S. potens*. A careful examination of the appropriate area, very well preserved in our specimen, fails to reveal any indication of its presence, or former presence.

The squamosal is of the large and characteristic dicynodont type, essentially triradiate in structure, with zygomatic, quadrate, and median rami; the convergent, ridged, upper or external surfaces of all three rami are highly rugose. Much of the structure of the median ramus has been noted in the description of the braincase. It consists for the most part of a vertical plate of bone applied to the anterior surface of the occipital plate. Dorsally this plate reaches forward around the upper border of the otic region below the lateral tip of the parietal. Above this region, close to the summit of the "occipital crest", is an area of bone of uncertain nature (marked "X" on Fig. 1), the surface of which is eroded. One possible interpretation is that it is a dorsal terminal prong of the squamosal with the tip of the parietal wedged between it and the main body of the bone. But a fracture across this region appears to show a definite separation between this region and the squamosal. This problematical area is applied to the anterior surface of the interparietal.but apparently a suture is present between them. Several alternative interpretations are still more unsatisfactory.

On its posterior aspect the medial ramus of the squamosal has ventrally a pronounced excavation into which is received the thickened distal end of the paroccipital process. More dorsally, the supraoccipital is ensheathed posteriorly, as well as anteriorly, by the squamosal, which has taken over many of the functions of the pelycosaur tabular. From the paroccipital buttress a pronounced ridge runs upward on the squamosal and curves medially above with more rounded contours. This ridge cannot have been developed for purely skeletal functions, and may mark the boundary of the area of insertion of the neck musculature. At the lower end this plate is applied anteriorly to the end of the pterygoid as well as the adjacent region of the quadrate.

The zygomatic ramus of the squamosal tapers rapidly to become triangular in section near the point where the zygoma ends in our specimen at a transverse fracture. The anterior tip of the bone is missing, but there is preserved the most posterior extremity of the jugal.

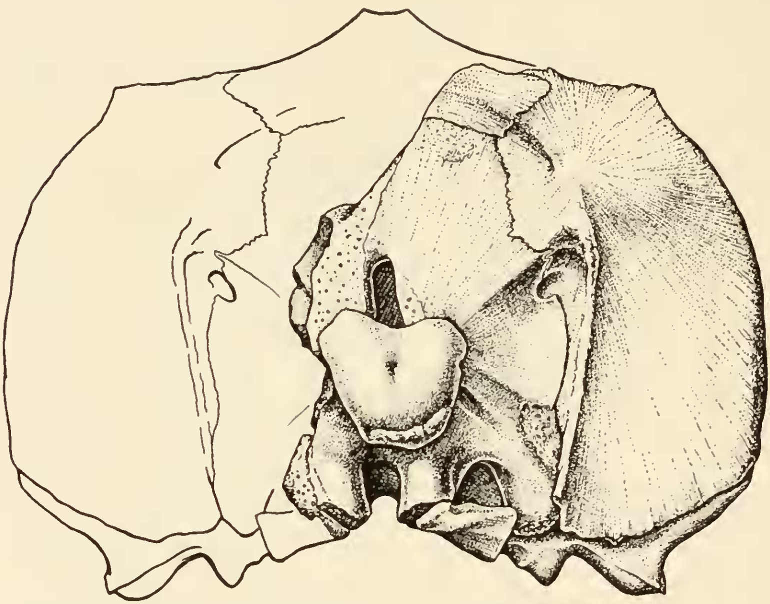

Fig. 3. As Figures 1–2, posterior view of right portion of skull; left side restored in outline. x 1/5.

The quadrate ramus of the squamosal as viewed from the posterior side is a flaring sheet of bone bounded medially by the vertical ridge adjacent to the occipital plate and with a thick and rugose lateral margin. In transverse section, this surface is concave near the medial margin; laterally the bone curves somewhat forward. It has been suggested that the corresponding posterior concave area of the squamosal in cynodonts is a groove for the external auditory meatus, but obviously such an explanation cannot fully account for the broad and high expanse of this region in dicynodonts. The ventral end of the plate becomes thin at its margin, which nearly reaches the articular surface of the quadrate, but does not occlude the quadrate foramen.

On the anterior surface the thick upper portion of this division of the squamosal forms, together with the base of the zygomatic ramus, a deep excavation which leads downward and forward toward the lower jaw. This fossa is suggestively similar to the temporal fossa lying on the opposite side of the zygomatic arch. Although the development of the quadrate ramus of the dicynodont squamosal may be explained functionally as due entirely to the necessity for support of the quadrate in its rotated position, it is not impossible that the fossa formed by its construction contained a specialized superficial division of the adductor musculature, comparable in mode of origin to the mammalian masseter, although radically different in function.

The ventral portion of the anterior surface of this ramus of the squamosal is cut into a distinct step in which is lodged the upper part of the quadratojugal. The smooth surface of the anterior face of the squamosal is continued downward without a break by the quadratojugal, and this bone laterally assists in the ventral prolongation of the lateral ridge on the squamosal. In our specimen, as apparently in von Huene's specimen of *S. potens* and various other described dicynodonts, the quadratojugal is slightly displaced, suggesting that the connection between squamosal and quadratojugal was not a close one; possibly a pad of connective tissue intervened. More medially the anterior face of the squamosal is in contact with the posterior surface of the quadrate. The situation is different here, however, from that concerned with the quadratojugal, for there is no "step" in the squamosal, but on the contrary a slight thickening, the quadrate being set out anteriorly beyond the plane of the squamosal.

The quadratojugal is a large element including a basal portion fused with the quadrate and a fan-shaped dorsal expansion which we have noted to be set into a step in the squamosal. The medial (morphologically posterior) border of the "fan" is apposed to the lateral margin of the quadrate for most of its length. Near the base the two bones separate to permit the formation of the quadrate foramen, which passes diagonally forward and inward between the two bones. No evidence of the suture between the base of the quadratojugal and quadrate described by Sushkin (1927, fig. 30) is visible in the specimen; presumably the quadratojugal terminates in a buttress above the lateral portion of the articular surface. Von Huene figures (1935, pl. 2) a ridge near the base of the bone which is not present in our skull, and a much greater lateral flaring above the neck region of that element.

The quadrate includes the articular region and a low rounded fan of bone extending upward above the medial portion of the articular area. As in synapsids generally the articular area consists of two convex portions. Separated by a diagonal groove, the lateral convexity is larger, but not markedly convex and faces rather medially, while the medial portion is smaller and more convex in section. Much of

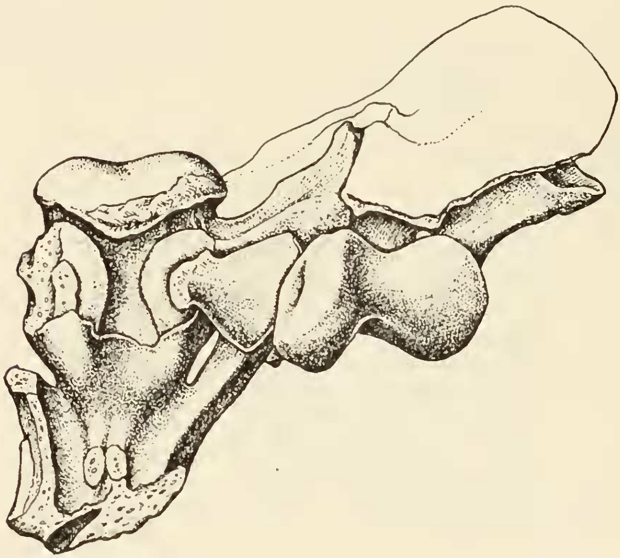

Fig. 4. As Figures 1–3, ventral view of braincase as preserved; right squamosal shown in outline only. x 1/4.

the "fan", ("otic process") rests, as we have noted, against the squamosal. Antero-ventrally, however, the distal end of the pterygoid is applied to its posterior surface in primitive fashion. The posterior portion only of the pterygoid is preserved. A distinct fissure, the primitive cranio-quadrate passage, is present between pterygoid and braincase. The distal end of the pterygoid ramus is slender and of no great height, but extends back to be clasped between the medio-ventral margin of the quadrate and the lower end of the squamosal. Anteriorly the pterygoids increase in height and thickness and the elements of the two sides are obviously applied in therapsid fashion to the sides of the basisphenoid. Ventrally in the pituitary region the two are separated by a cavity which represents the hollow primitively present between the basipterygoid processes. Ventral again

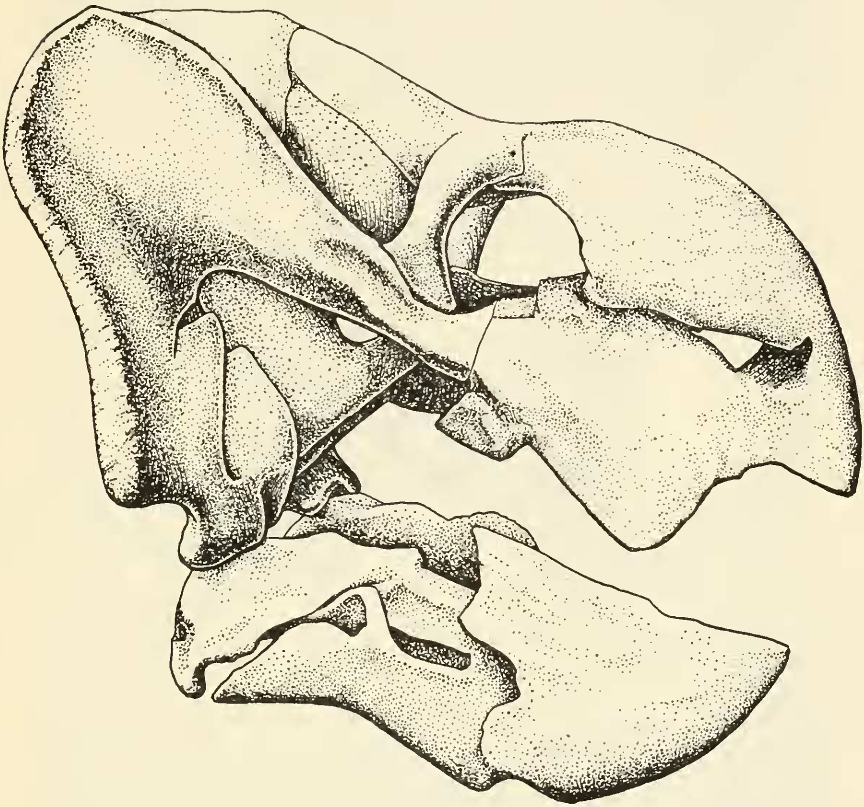

Fig. 5. *Stahleckeria potens*, lateral view of skull. x 1/6 approx. After von Huene.

to this the two bones are in apposition and appear to send back a pair of short posterior extensions. Details of construction are none too clear here and the more anterior extensions of the pterygoids are missing.

The ascending process of the epipterygoid is well preserved. It is thin and moderately expanded antero-posteriorly. Dorsally there is a well-defined suture with the parietal; below this point the anterior and posterior margins are free to stand well out from the level of the braincase wall. From the base of the "columella" a well-ossified posterior extension of the epipterygoid runs back above and lateral to the pterygoid in the direction of the quadrate. As preserved, the bone does not quite reach the latter element, but a connection may have been present in life. There appears to have been a considerable extension of the epipterygoid over the lateral surface of the pterygoid

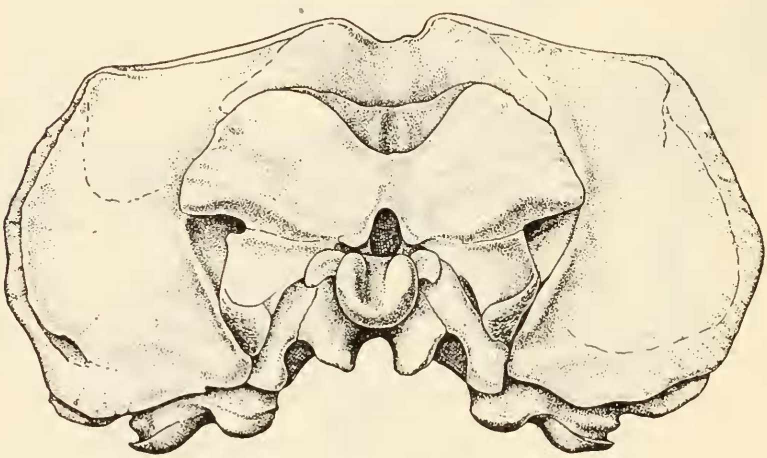

Fig. 6. *Stahleckeria potens*, posterior view of skull. x 1/6 approx. After von Huene.

below the "columella", but the ossification is feeble. However there is a distinct groove on the lateral surface of the pterygoid for the posterior extension of the foot. Anteriorly the foot is broken off as is frequently the case in dicynodont material. The right stapes is present in natural position in our specimen, as well as a fragment of the left. It is very short but stout. The oval footplate is present nearly in proper position covering the fenestra ovalis. Thence the bone runs laterally and expands distally to abut (as preserved) on to the medial margin of the articular region of the quadrate, to touch dorsally the lower edge of the tip of the paroccipital process, and to lie close behind the distal end of the pterygoid. A groove crosses the dorsal surface just lateral to the footplate; there is no evidence of a foramen.

The partial skull described above is obviously comparable in many regards with the material described by von Huene as pertaining to *S. potens*.[1] We have, however, noted a number of features in which our specimen appears to differ. Many of these are probably to be attributed to varied imperfections in the material in both cases and consequent differences of interpretation. In a few regards, however, differences seem to be more concrete. The complete skull figured by von Huene (his Pls. 2, 3) is definitely much broader than ours. Using the width of the condyle as a basis for comparison, this measurement is contained in the estimated total width only 5½ times in our specimen; 9 times in his skull. Some part of this difference might be attributed to differential crushing, but certainly not all. With this contrast in total proportions are associated differences in the proportions of the component elements of the occiput. In addition, *S. potens* appears to have a relatively broad and flat area between the temporal vacuities. Our specimen appears to have had a more sharply developed "sagittal crest"; however, the evidence for this is indirect and none too positive.

POSTCRANIAL SKELETON

The remains of the postcranial skeleton pertaining to this individual include a single vertebra; a tibia; and much of the left front leg and shoulder, including a nearly complete scapula and the lower end of the humerus in natural articulation with the forearm and foot.

Vertebra (Fig. 7). The single vertebra preserved has a length of centrum of 95 mm., a width of 133 mm. across the posterior face of the centrum and a total height to the tip of the neural spine of approximately 420 mm. These figures compare with maximum measurements given by von Huene of 74 mm., 102 mm. and 300 mm.; our vertebra exceeds any cited by him by one-third. It will be seen that the limb material of our specimen exceeds in size any of the elements in von Huene's collection, but the differences are of a smaller order. It is possible, however, to reconcile this situation by calling to attention the fact that the vertebrae and limb bones measured by him, many of which form part of his mounted skeleton, may have been associated with his skulls nos. 1 and 2. His skull no. 3 is about 20% larger than the others and may well have been carried by a larger column. We may further note that while our vertebra probably comes from the

[1] Since von Huene's work is not generally available, we give here modified reproductions of two of his figures (Figs. 5, 6).

same individual as the other material here described, it was not actually articulated.

Rib (Fig. 7). Of the rib system, only a single fragment was preserved. This is the proximal part of a posterior cervical or anterior dorsal of the right side. Distinct capitular and tubercular attachments are present. The capitular facet is essentially circular, with a diameter of about 40 mm.; the tubercular facet is elongate; length of the articular face is 84 mm. and the total breadth of the proximal end of the rib 132 mm.

Scapula (Fig. 8). A nearly complete right scapula is present. The lower margin is somewhat imperfect and eroded. The blade has been subjected to some antero-posterior pressure so that a longitudinal fold, obviously post-mortem, extends along it for some distance. Otherwise the element is well preserved and shows good surface detail in many regions. The specimen is of large size. Despite the fact that it is incomplete ventrally, the length along the convex surface is 555 mm. and the length by direct measurement 505 mm. If the bone were complete, these measurements would have been on the order of 600 and 540 mm. Comparable figures for two complete and presumably adult specimens in von Huene's possession are 600 and 555 mm. for the convex length, 540 and 500 mm. for the direct measurement.

The general proportions agree well with von Huene's figures of his "specimen 2". The acromion is thick, with a rounded massive terminus for clavicular articulation, and is not as distinctly set off from the spine as in his "specimen 1". On the latter von Huene notes a deep groove at the thick upper end of the anterior margin of the scapula which he suggests may have lodged a cleithrum. Our specimen is well preserved in this area; the edge is thin and shows no indication of such a groove. This is also the case with von Huene's two remaining specimens, and we are thus inclined to believe that this furrow is a post-mortem effect; his figures suggest that the whole anterior edge of "specimen 1" has been subjected to considerable crushing and distortion. A groove for cleithral articulation is noted by Pearson (1924a, pp. 832–833) in *Kannemeyeria*, but this was for the lower end of the cleithrum; the area corresponding to von Huene's groove is a convex surface in *Kannemeyeria*. The upper edge of the scapula is a diagonal line slanting downward from back to front, with a sharp postero-dorsal corner and an obtuse antero-dorsal corner. This is in pronounced contrast with von Huene's specimens where the upper edge is essentially horizontal. Our specimen suggests (but by no means proves) a more posteriorly inclined position for the scapula than is advocated by von

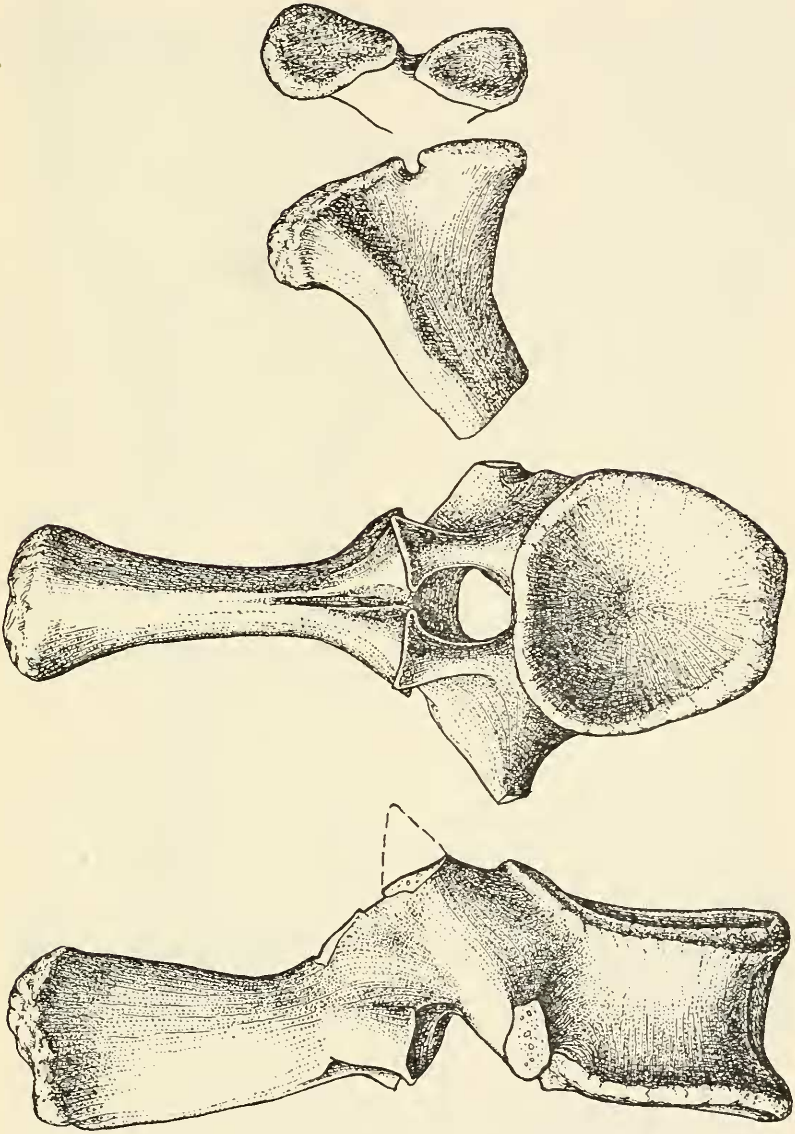

Fig. 7. *Stahleckeria lenzii.* Left, vertebra, right lateral and posterior views. Right, proximal portion of a right cervical rib. x 1/4.

Huene for *Stahleckeria* or by Watson and Pearson in other genera. This upper margin is gently convex in outline and is apparently an "unfinished" surface; presumably there was a small cartilaginous suprascapular area.

The posterior margin of the blade is quite thick. The spine is high and well developed. It is rugose along the summit for its entire length. This rugose area is broader proximally, narrower distally, and obviously was the area of attachment of the scapular portion of the deltoid muscle. Presumably the trapezius muscle attached, as usual, to the original line of the cleithrum rather than to the anterior face of the spine; here, as first pointed out by Watson, we would expect a muscle comparable to the mammalian supraspinatus. This anterior surface of the spine passes down smoothly beneath the acromion and out ventrally to the external surface of the girdle in a fashion appropriate to the supraspinatus channel. This surface is stated by von Huene to be interrupted by a sharp cross-ridge in his "specimen 1" and by a process higher up in his "specimen 2". Nothing of the sort is present in our specimen (the surface here is well preserved) and the effects noted by von Huene may be post-mortem.

Our specimen appears to exhibit a foramen entering the bone from the external surface somewhat anterior and ventral to the acromion. Von Huene's figures of "specimen 1" suggest a similar structure. It is not impossible that this is a surviving supraglenoid foramen, but nothing of this sort is known in other dicynodonts and it may be a nutrient foramen or (since the surface is not too well preserved in this area) an artifact.

Humerus. The distal end only was preserved, this being found in natural articulation with radius and ulna. It measures about 30 cm. across the condyles and is thus about the size of von Huene's largest specimens. As far as preserved it appears to agree well with his descriptions of the *Stahleckeria* material.

Radius (Fig. 9). A right radius is present and nearly complete, lacking only a few chips from the proximal end. The length is approximately 29 cm. Von Huene figures an incomplete and considerably restored specimen of *Stahleckeria* with an estimated length of 22 cm. He believed that his specimen was that of the left side, and that the aspect figured was the dorsal surface. Our complete specimen suggests that his interpretation was in part correct, but that the orientation of the distal end was reversed, his supposed ventral surface being actually the dorsal aspect.

The proximal articular surface is well cupped, and flares widely

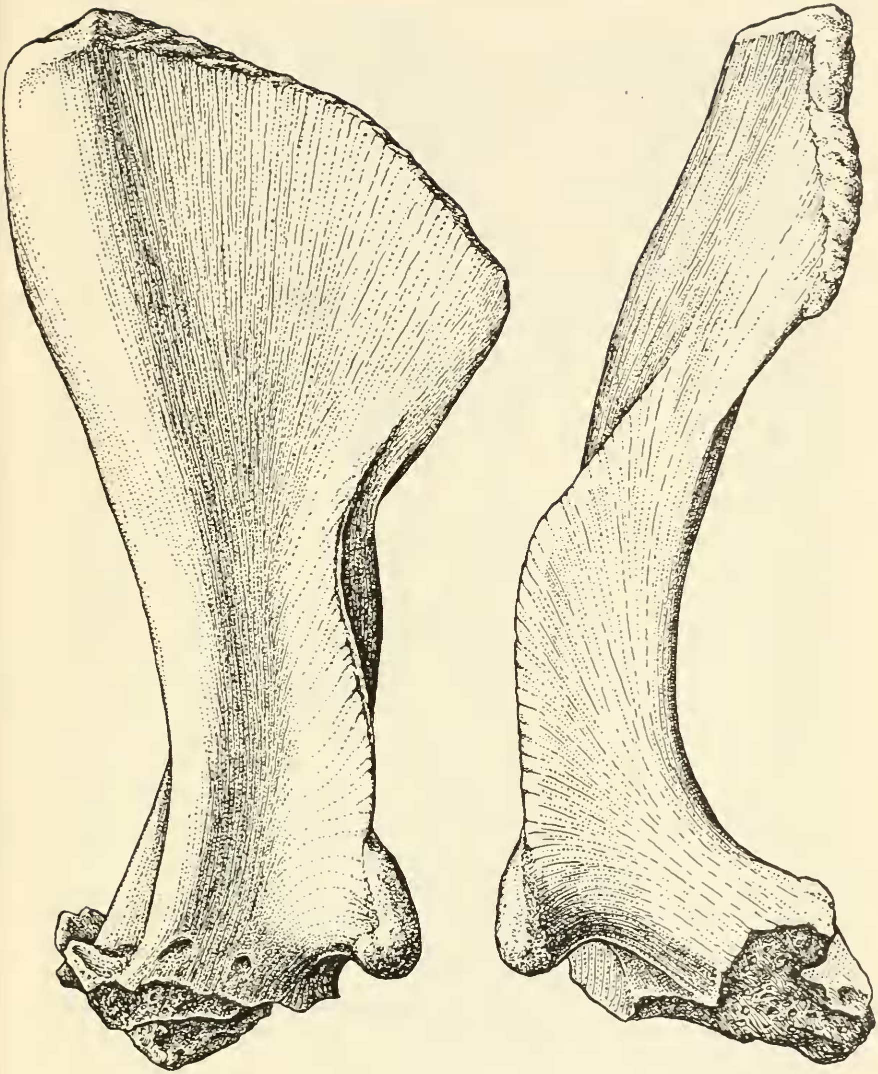

Fig. 8. *Stahleckeria lenzii*, right scapula. x 1/4.

toward the medial side. This medial expansion is incomplete in our specimen; as preserved the width of the head is 15 cm., as contrasted with 14 cm. in von Huene's specimen. The shaft is flattened dorsoventrally, the breadth at the narrowest portion being 75 mm. and the thickness only about 50 mm. The distal end is greatly expanded toward the medial side, extending far beyond the radiale and having a width of 18 cm. (as compared with von Huene's estimate of 12 cm.). In its distal portion the bone is relatively thin toward the medial margin and thicker laterally, so that the shaft here presents a distinct, flattened, ventro-lateral aspect as well as extensor and flexor surfaces.

Ulna (Fig. 9). The complete right ulna has a total length of 56 cm.; from the bottom of the sigmoid notch to the distal end measures 32 cm. These figures indicate a size considerably in excess of the largest of von Huene's specimens, in which the comparable measurements were 49 cm. and 25 cm. respectively. Apart from differences due to variation in preservation and crushing, our specimen agrees rather well with that of von Huene. This is described as a left, but as seen from his plate 7, fig. 8, it is very similar to ours which is part of an articulated right limb.

In most described dicynodont material the olecranon is undeveloped in ossified form and hence perhaps none too large in life. In contrast is the enormous development seen in our specimen and that figured by von Huene, in which the olecranon and sigmoid notch occupy nearly half the length of the bone. The olecranon is completely ossified here, the bone terminating dorsally in a relatively narrow ridge. This ridge curves ventrally toward the outer margin, so that the flexor aspect of the olecranon is concave, in general primitive reptilian fashion. Opposite the sigmoid notch region the lateral margin of the shaft is thick and rounded; more distally this margin is sharper. On the extensor aspect the bone is convex both in the olecranon region and distally; opposite the sigmoid notch lies a concavity. This last may be due to crushing, as is surely the longitudinal furrow seen on the extensor aspect of von Huene's specimen. A deep concavity on the flexor aspect of the shaft of our specimen opposite the lower end of the sigmoid notch is surely due to crushing. Little can be said with certainty of the details of the sigmoid notch because of the poor surface present here. There is a distinct area for articulation with the head of the radius; this area is well seen also in von Huene's specimen.

Manus (Figs. 9, 10). Von Huene's specimens included almost no foot material. Our specimen includes a right manus, articulated and nearly complete except for the terminal phalanges. As would be expected, this foot is of enormous size, with an estimated length of 47 cm. and an estimated spread across the toes of about 45 cm.

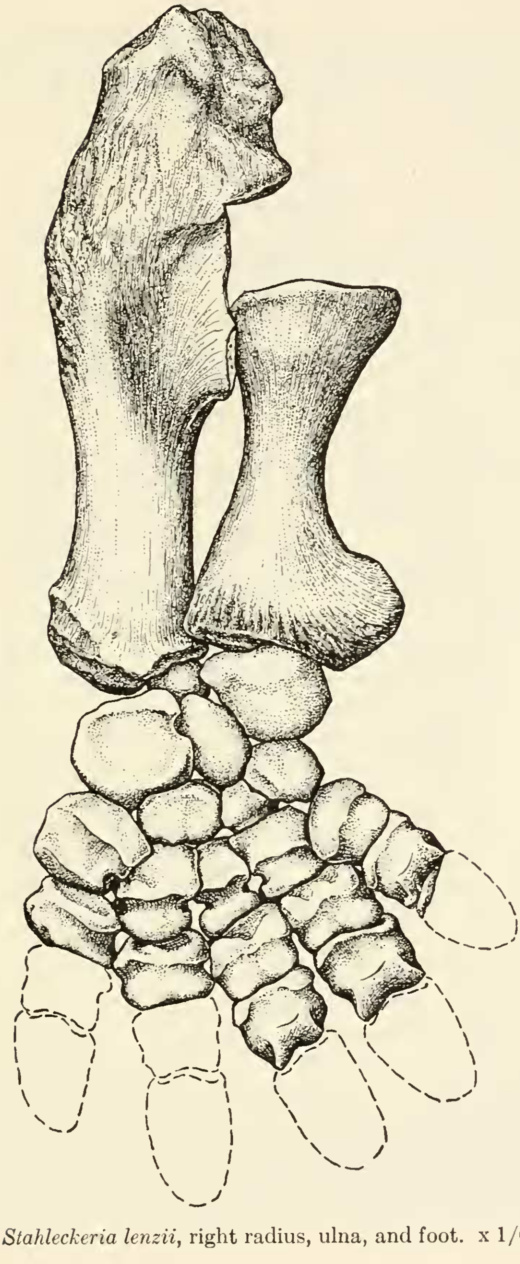

Fig. 9. *Stahleckeria lenzii*, right radius, ulna, and foot. x 1/6 approx.

The structure of the dicynodont foot is none too adequately known and it is hoped that a study of the foot material of the various dicynodonts in the Museum's Brazilian collection may aid in its interpretation. For the present we shall, for the most part, confine ourselves to a description of the specimen at hand.

The proximal row of carpals is present. The radiale is somewhat triangular in dorsal and ventral aspects, with the apex of the triangle toward the lateral side and the base of the triangle the rounded medial margin. The bone is thin medially but becomes increasingly thick laterally. The proximal margin is in contact with the distal end of the radius. Distally there is a broad face which may be presumed to have been in contact with a cartilaginous medial centrale.

The outlines of the intermedium are poorly preserved. The bone appears to have been subquadrate in shape, with a longitudinal hollow along the ventral surface.

The ulnare is essentially rectangular, with a width half again as great as the length. The proximal end is much thickened medially, becoming thin laterally. The same is true of the distal end, and the entire lateral margin is thin. Most of the distal surface was surely in contact in life with the fourth distal carpal. As preserved the fibulare appears to abut to a considerable extent on the fifth metacarpal. But it is probable that the carpals are somewhat displaced laterally on the digits and that little, if any, contact of this sort was present in life. On the medial aspect of the ulnare there is a well-developed notch which presumably served, as in early reptiles generally, for the passage of the perforating artery.

No pisiform is present; it might have been present in cartilage.

A lateral centrale is present in its typical position, below the intermedium and between radiale and ulnare. Little can be said of the details of its structure. No medial centrale is preserved, but it is reasonable to assume that it was present in cartilage.

Of the distal carpals, three are present. There is no evidence of a fifth member of the series, although it may have been present as a small cartilage. The fourth is, as usual, a large element, seen nearly in proper position beneath ulnare and lateral centrale. Distally, presumably owing to displacement, it appears to articulate to a considerable extent with metacarpal 3 as well as the more lateral elements with which it normally articulates. Distal carpal 3 is a relatively small element and, like the fourth, is displaced medially so that as preserved it is opposite metacarpal 2. Adjacent medially to metacarpal 3 is a large element. We suggest that distal carpal 2 was present in cartilage only or has been lost and that this large element is the first distal carpal. Distal carpal 1 would tend to be better ossified because of the fact that it partakes in great measure of the

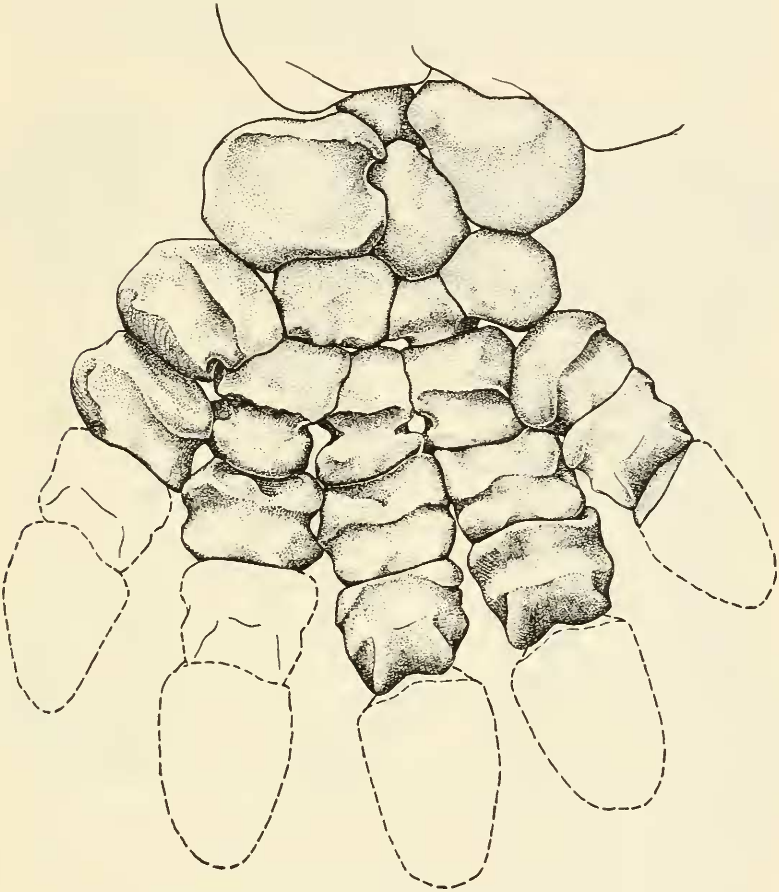

Fig. 10. *Stahleckeria lenzii*, right manus, dorsal view. x 2/9.

functions of a metacarpal. Its surfaces are poorly preserved and hence detailed description is impossible.

The carpal structure, as described above, is not dissimilar to that which appears to have been present in earlier Karroo dicynodonts. There is considerable variation in the degree of ossification of the more distal elements in the few forms described in this regard from South Africa.

The metacarpals and phalanges are exceedingly broad and short. A strong tendency in this direction is general in dicynodonts, and would be expected to be emphasized in a graviportal type such as the present one. The phalangeal formula is obviously, as usual, 2·3·3·3·3.

The general description of these elements which follows applies to digits 2–5. The proximal articular surfaces of the metacarpals are very broad and nearly flat. On the sides of the heads of each are well-developed articular areas which are apposed to the adjacent metacarpals, making for solidity of structure and relative immobility of the individual digits. Beyond a markedly constricted "waist" the typical metacarpals exhibit an oval and almost uniformly convex, distal, articular area.

The non-terminal phalanges are shorter than the metacarpals and with a less constricted "waist". The proximal articular surfaces of the first phalanges are concave in dorsoventral section. In horizontal section the surface is in general likewise concave, but consists essentially of paired swellings, separated by a median groove. The distal articular surfaces of the first phalanges are convex in both dimensions and consist of paired elevations with a slight depression between them.

The proximal articular surfaces of the second phalanges are paired concavities with a median ridge between them. The distal surfaces, articulating with the unguals, extend far on to both dorsal and ventral surfaces of the phalanges. On each phalanx the distal articulating surface consists of a pair of keels which form practically a semicircle; they are separated by a deep median groove. A circular pit is present within the surface enclosed laterally by the lateral keel. In contrast to the more proximal joints, that connecting the unguals was obviously one permitting considerable freedom of motion.

Almost no remains of the unguals are preserved; isolated elements noted by von Huene show that they were of the typical broad and flattened dicynodont type.

The first digit here, as in primitive reptiles generally is peculiar in that there is a proximal shift in the nature of the elements, which may be of importance in the history of the foot (a point which we may discuss on some future occasion). The metacarpal partakes in considerable measure of the nature of a "normal" first phalanx, and the first phalanx is comparable to the second phalanx of the more lateral digits.

Tibia (Fig. 11). A complete right tibia has a length of 38 cm., as compared with a length of 34 cm. in the single tibia available to von Huene. As he notes, his specimen is obviously pathological in structure; ours is more normal in build. The head is a massive subcircular structure, slightly concave, from the general contours of which the

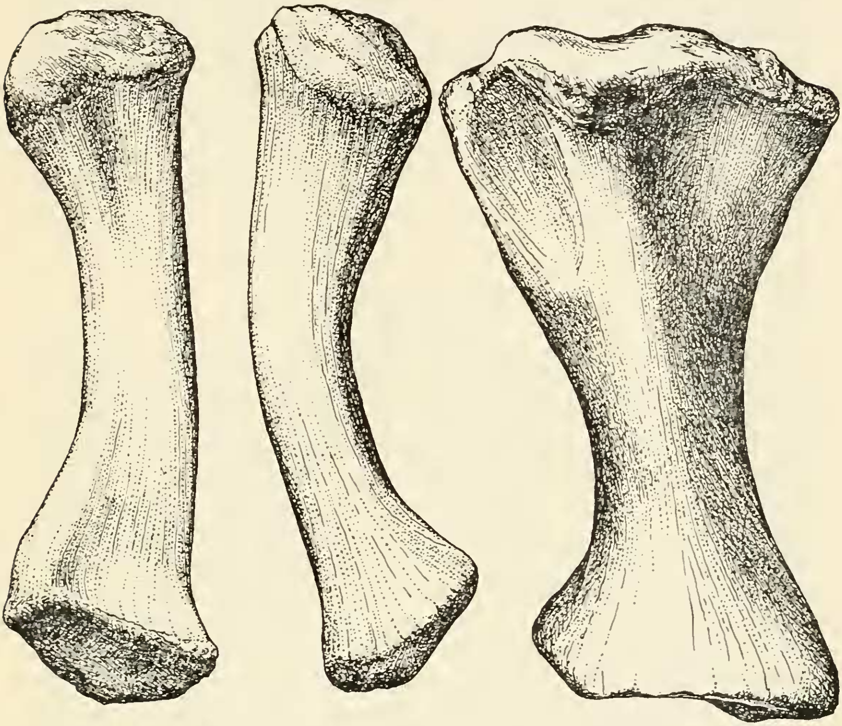

Fig. 11. *Stahleckeria lenzii.* Left, right fibula, flexor and extensor aspects. Right, right tibia, extensor aspect. x 1/4.

cnemial crest projects but little; the transverse width is 21 cm. The distal articular surface is likewise concave and is subcircular in outline, with a transverse width of 15 cm.; this surface is tilted somewhat toward the lateral aspect.

Fibula (Fig. 11). The fibula described by von Huene has a most abnormal appearance and, like the tibia, is probably pathological in its proximal portion. There is available to us a single right fibula, from the same locality as the specimen from which our other materials are derived, but not definitely associated with it. The two ends are preserved but there is no contact in the middle of the shaft. Obviously, however, little is missing for the total length of the two portions present is 35 cm., as compared with but 32 cm. in von Huene's complete specimen. The greatest diameter of both proximal and distal articulations is 11 cm., as compared with 10 cm. and 9 cm. in von Huene's specimen. The proximal articular area is of a general, primitive, reptilian shape, an oval with a somewhat curved axis, and is moderately convex. The distal articular surface is subcircular and convex. In its lower part the shaft exhibits an extensor surface strongly convex in section. The lower portion of the flexor surface is flattened, but the bone here flares strongly outward at the distal end.

DISCUSSION

The specimen described above obviously represents a gigantic dicynodont, similar in size to the individuals described by von Huene as *Stahleckeria potens,* and similar also in many anatomical features. We were at first inclined to attribute our material to von Huene's species, particularly since it comes from the same general region and from a horizon which is not improbably the same. However, detailed study shows a number of differences, particularly in the skull, as noted earlier, and many of the resemblances are simply features which might be expected in any dicynodont of large size. The differences may be in part individual and sexual, in part due to imperfections and differences in mode of preservation of the material. Nevertheless they are considerable, and lead us to believe that our specimen is specifically and quite possibly generically distinct. As the more conservative course we shall, until further data is available, consider it as pertaining to *Stahleckeria,* and describe it as *Stahleckeria lenzii,* sp. nov., distinguished from the genotype by such cranial features as the relatively narrower occiput and more compressed parietal region. The specific name is given in honor of Colonel Albino Lenz, of Candelaria, to whom we are grateful for many favors done the Harvard Expedition.

In a consideration of the relationships of *Stahleckeria,* one tends primarily to compare the genus with other large Triassic dicynodonts. Several forms of this sort are known, *Kannemeyeria,* (Pearson, 1924 1924a, Case 1934) of the early Triassic of South Africa, *Placerias* o the western United States, and *Sinokannemeyeria* of China (Young, 1937). Von Huene suggests that *Stahleckeria* is a "modified" *Kannemeyeria*, that the two are quite similar in structural features, but differ in cranial proportions, and implies that the skull type seen in *Kannemeyeria* is a relatively primitive one, from which that of *Stahleckeria* may have been derived.

We find it difficult, however, to accept this point of view. A few similarities between the two genera, such as the apparent absence of the preparietal, may be cited; but the contrasts are great:

(1) *Kannemeyeria* is slender-snouted, with an elongate, ridged, premaxillary region; *Stahleckeria* has a broad, short snout.

(2) *Kannemeyeria* has well-developed tusks; *Stahleckeria* appears to lack them, but has instead a prominent bony boss in the canine region.

(3) In *Kannemeyeria* the squamosal region is very strongly produced posteriorly, resulting in an exaggeration of the V-shaped contours of the lower margin of the skull and in a strongly concave occipital plate; in *Stahleckeria* the squamosal has relatively little extension backward and the occiput is nearly vertical.

Certain of these features do not, of course, bar *Kannemeyeria* from the ancestry of *Stahleckeria;* a tusked condition is obviously more primitive than a tuskless one, and although broad-snouted dicynodonts appear early in the history of the group, a slender-snouted stage may well have been an antecedent one.

As regards the posterior portion of the skull, however, we find it difficult to believe that *Stahleckeria* can have been derived from a *Kannemeyeria*-like form. The curvature of the lower border of the skull in the squamosal-quadrate region is a development seen in therapsids in general and related to the nature of the jaw-closing apparatus. It is much more marked in dicynodonts than in other groups, producing here the characteristic V-shaped lower margin of the zygomatic arch. The modest development of this peculiarity in *Stahleckeria* is a relatively primitive condition which contrasts strongly with the exaggerated development seen in *Kannemeyeria*. It is possible that a reversal of this evolutionary trend occurred, but it is not at all probable.

All in all, it seems probable that the two genera merely represent two independent "phyla" of large Triassic dicynodonts, which may have quite different relationships.

It would be of interest to be able to compare *Stahleckeria* with *Placerias* of North America. However, described remains of the latter genus include only the single limb bone forming the type and possibly, certain isolated elements described by Williston from Wyoming. Camp (1934) has recently discovered an abundance of material of *Placerias*, and attempts at comparison must be postponed until this is described. It is possible that *Placerias* is related to either *Kannemeyeria* or *Stahleckeria*, but equally possible that it may prove to represent still a third end-form expressive of a tendency toward gigantism in the late survivors of the dicynodont group.

Although the phylogenetic relationships of the multitudinous Karroo dicynodonts are as yet poorly understood, certain of the described South African Permian types are apparently rather more suggestive of *Stahleckeria* than is *Kannemeyeria*. Of interest is the genus *Aulacocephalodon*, as interpreted by Broom to include "*Dicynodon*" *tigriceps* and a number of other species. These forms were already of considerable size; a skull of *A. peavoti* in the University of Chicago collections measures 470 cm. in length (Olson and Byrne 1938) and is thus not far below that of *Stahleckeria* in size. In this genus the preparietal is still present, tusks are present in many specimens and there is a tendency for the development of rugose areas on the nasals and prefrontals. In other respects, however, such a form as *A. peavoti* appears to agree well with *Stahleckeria*. Common, and perhaps significant, features include the short, broad muzzle, the lack of marked posterior extension of the squamosal and the nearly vertical occiput.

Still more probable, however, is the supposition that *Stahleckeria* is a "local product". There exists in the same beds a considerable fauna of dicynodonts of smaller size, which for the most part are as yet undescribed. *Stahleckeria* appears to resemble these forms in many regards. The genus may be merely a development of gigantism in a regional fauna and lack any intimate genetic connection with "giants" of other continental areas.

BIBLIOGRAPHY

CAMP, C. L.

1934. New Reptile Fauna from the Chinle Triassic of Arizona. (Abstract). Proc. Geol. Soc. Amer., for 1933, pp. 392–393.

CASE, E. C.

1934. Description of a Skull of *Kannemeyeria erithrea* Haughton. Contr. Mus. Paleont., Univ. Michigan, **4**, no. 7, pp. 115–127.

HUENE, F. VON.

1935. Die fossilen Reptilien des Südamerikanischen Gondwanalandes an der Zeitenwende, Ergebnisse der Sauriergrabungen in Südbrasilien 1928–29, Lief. 1, pp. 1–92.

HUENE, F. VON.

1936. Ein *Stahleckeria*-Schädel. Zentralblatt. f. Min. etc. Jahrg. 1936, abt. B, No. 11, pp. 507–509.

OLSON, E. C. and BYRNE, F.

1938. The Osteology of *Aulacocephalodon peavoti* Broom. Jour. Geol., **46**, no. 2, pp. 177–190.

PEARSON, H.

1924. The Skull of the Dicynodont Reptile *Kannemeyeria*. Proc. Zool. Soc. London, 1924, pp. 793–826.

1924a. A Dicynodont Reptile Reconstructed. Proc. Zool. Soc. London, 1924, pp. 827–856.

SUSHKIN, P. P.

1927. On the Modifications of the Mandibular and Hyoid Arches and their Relations to the Brain-case in the early Tetrapoda. Palaeont. Zeitschr., **8**, Heft 4, pp. 263–321.

YOUNG, C. C.

1937. On the Triassic Dicynodonts from Shansi. Bull. Geol. Soc. China, **17**, nos. 3 and 4, pp. 393–411.